

PRE-NESTING AND NESTING BEHAVIOR OF THE SWAINSON'S WARBLER

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THE Swainson's Warbler (*Limnothlypis swainsonii*) is one of the least known of southern birds. Although fairly common in some parts of its range, observations of its breeding biology have been made by few persons. Substantial observations have been made by J. Fred Denton at Augusta, Georgia (Griscom and Sprunt, 1957:50-53), and by Eleanor Sims at Charleston, West Virginia (Sims and DeGarmo, 1948:1-8).

I made observations on breeding behavior, mainly during the years 1963-1967, in canebrakes (*Arundinaria gigantea*) along the Ocmulgee River about 5 miles south of Macon, Bibb County, Georgia; in canebrakes along the Arkansas River about 5 miles north of Pendleton Ferry, Arkansas County, Arkansas; and in deciduous thickets composed mainly of sweet pepperbush (*Clethra alnifolia*) and greenbrier (*Smilax rotundifolia*) in the Dismal Swamp, Nansemond County, Virginia. A few observations were made near Macon during the mid-1940's, and at Alexandria, Rapides Parish, Louisiana, during the mid-1950's. For a description of Swainson's Warbler habitat at these stations see Meanley (1966).

METHODS

All observations were made with binoculars. The size of a territory was determined by repeatedly locating the male on either side of lines 50 feet apart.

Several females were color-marked after they were captured by flushing them from their nests into mist nets. Males were captured for color-marking by mist netting in their territories.

ARRIVAL ON BREEDING GROUNDS AND PAIRING OF BIRDS

In central Georgia, central Louisiana, and east-central Arkansas, Swainson's Warblers arrive on their breeding grounds chiefly during the first two weeks of April. They are one of the last of the southern breeding warblers to arrive, but they are earlier than the northern transient warblers.

A local male population arrives at its breeding ground during a period of about one week. At Macon in 1966, the season being late, the first males (four) arrived in my study area (100 acres) on 12 April; by the next morning there were eight males; nine on the 14th; and 10 on the 15th, the date I departed from the area. When I returned on 28 April, there were 19 males in the area.

Sprunt and Denton (Griscom and Sprunt, 1957:51) stated that females arrive about 10 days later than males. Further evidence that males migrate ahead of females is provided by seven birds that struck a television tower

TABLE 1
SIZES OF SWAINSON'S WARBLER TERRITORIES

Locality	Size (acres)	Reference
Ocmulgee Riverbottom, Bibb Co., Ga.	0.3	author
Monkey John Swamp, Jasper Co., S. C.	0.6	author
Savannah Riverbottom, Richmond Co., Ga.	0.72	Griscom and Sprunt (1957)
Savannah Riverbottom, Richmond Co., Ga.	0.79	Griscom and Sprunt (1957)
Ocmulgee Riverbottom, Bibb Co., Ga.	0.83	Griscom and Sprunt (1957)
Little River Swamp, Tift Co., Ga.	0.91	Griscom and Sprunt (1957)
Dismal Swamp, Nansemond Co., Va.	1.7	author
Dismal Swamp, Nansemond Co., Va.	3.9	author
Dismal Swamp, Nansemond Co., Va.	4.8	author

north of Tallahassee, Florida, in 1966. The birds were picked up at the base of the tower by H. L. Stoddard, Sr., as follows: 4 April, two males; 15 April, one male and three females; and 19 April, one female.

When I visited my study area at Macon on 4 April 1967, Swainson's Warblers had not yet returned. Nine days later (on the 13th), I revisited the area and found 12 males on their breeding territories. Of these one male was paired. I could tell from the frequency of the singing of males that most of the birds were not yet paired. Seven paired males that I have observed during pre-nesting in various localities sang less often than at other times during the breeding season. At Alexandria, Louisiana, a color-marked male that arrived on 3 April was paired by 17 April.

TERRITORY

Size of territories.—During the breeding season Swainson's Warblers were found in groups or "colonies," like Kirtland's Warblers (*Dendroica kirtlandii*) (Mayfield, 1960:2); as isolated pairs; or as unmated males, isolated, or in "colonies." The sizes of territories where birds occur in groups usually are smaller than where isolated birds are found (Table 1). For example, the territory of one isolated pair in the Dismal Swamp covered nearly five acres, the territory of another pair nearly four acres. However, in an area in the Ocmulgee River floodplain forest there were four territories on seven acres, and some of the seven acres was unoccupied.

The smallest Swainson's Warbler territory that I measured contained only 0.3 acres. It was located in a block of woodland approximately two acres in size, and it was separated from the main forest by a cleared power-line right-of-way 50 yards wide. An unmated male occupied this territory during most of the breeding season.

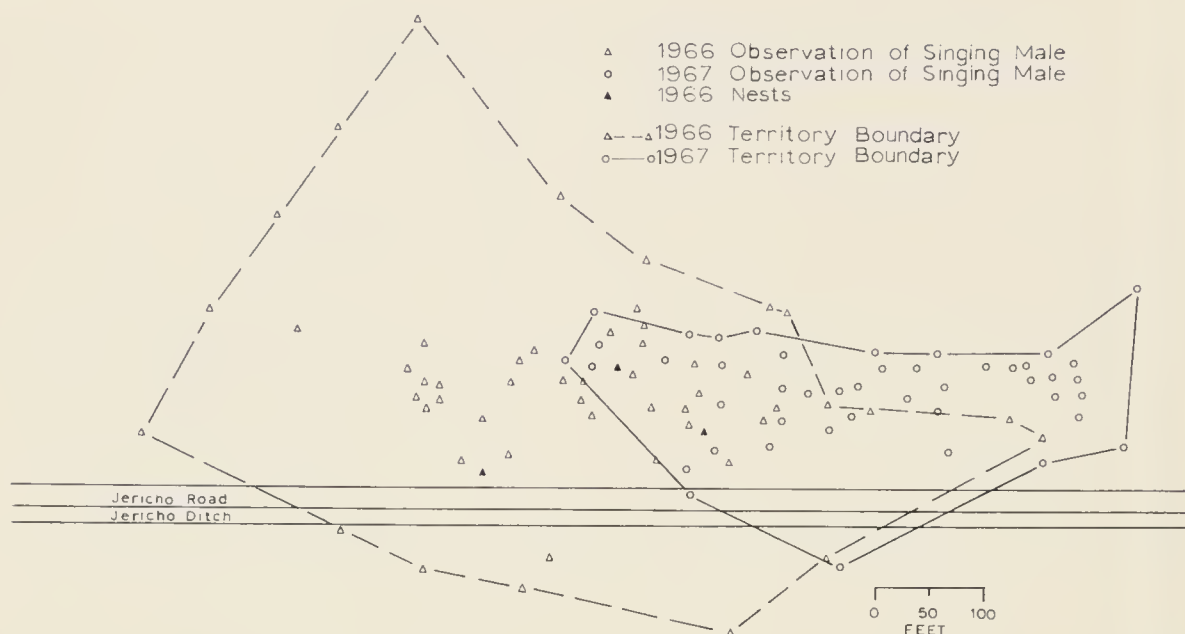


FIG. 1. Territories of a male Swainson's Warbler during the middle of June in consecutive years (1966 and 1967) in the Dismal Swamp, Virginia.

Sometimes in such non-continuous habitat males occupy split territories or territories composed of separate segments. One territory in Monkey John Swamp near Savannah, Georgia, had three segments. Two of the segments were on opposite sides of a cypress (*Taxodium distichum*) pond; the third was across a road from the pond. The occupied segments totaled 0.6 acres.

In an isolated territory of a pair of Swainson's Warblers in the Dismal Swamp, the section with the least understory (3.5 acres) was occupied only 30 per cent of the time; while the part of the territory with the most understory (1.3 acres) was occupied 70 per cent of the time. The female's three unsuccessful nests were located in the 1.3-acre section.

Apparently there is variation in the sizes of the territories of some passerines during the breeding season, but I have been unable to map territories of the Swainson's Warbler throughout the breeding season to show this. Stenger and Falls (1959:136) found that the area utilized by male Ovenbirds (*Seiurus aurocapillus*) was larger during the premating, mating, incubation, and nestling periods than during nest-building and egg-laying. I have observed that some male Swainson's Warblers occupy larger areas during the first day or two following their arrival on the breeding grounds.

It is well known that individuals of many species may return to the same general area in successive years. During my study, a marked male Swainson's Warbler occupied a territory in the Dismal Swamp in 1967 which was adjacent to and partially overlapping his 1966 territory (Fig. 1).

Territorial Behavior.—Males establish territories almost immediately after their arrival on the breeding grounds. One color-marked Arkansas male occupied the same territory for at least four months (15 April–15 August). Its mate disappeared after one unsuccessful nesting attempt.

Territories are defended through use of song, chasing, and combat (Meanley, 1968). Hostile encounters between Swainson's Warblers usually take place along the boundary of adjacent territories. Observations of such encounters were based mainly on the activities of paired versus unpaired males. The four paired males were more aggressive than the five unpaired males and usually initiated the border encounters. A territorial male with an incubating mate at Pendleton Ferry, Arkansas, apparently had more time for hostile activity and thus was involved more often than a paired male at Macon, that was travelling with its mate during pre-incubation. Six hostile encounters between the same neighboring paired and unpaired males at Macon took place at a single point along the boundary.

The Arkansas male would fly from any point in its territory to start a fight at the mutual boundary. It would start *chipping* excitedly as it moved toward the boundary. Both males *chipped* constantly during border clashes. In addition to chasing, the birds fluttered about on the ground after making contact, and sometimes flew together a few feet up from the ground grasping at each other's bills. At Macon, as the males chased each other along the boundary, the paired female was close by but remained 10 to 15 feet within her territory, *chipping* excitedly.

Toward the end of an encounter the Arkansas male usually performed a display near the boundary, in which the wing and tail feathers were spread and the tail vibrated. Sometimes he would side-step back and forth along a branch emitting loud and soft *chips*. I have observed this display given by several males. Ficken and Ficken (1962:110) observed a somewhat similar display in the Redstart (*Setophaga ruticilla*) after prolonged encounters.

Following boundary encounters males drifted back onto their territories and usually sang unbroken courses of songs for several minutes. Sometimes males started singing close to the boundary in which case the songs were incomplete, consisting only of the first two or three notes. Then as they moved farther into their respective territories they sang complete songs. Sometimes following a border encounter, each time one of the males sang, the other would utter a *zeep* note.

There was usually little antagonism toward other species and vice versa.

PRE-NESTING ACTIVITY OF PAIRS

Most of my information on activities of paired birds before nest building is based on observations made 13 and 14 April 1967 of a pair on their

territory in a canebrake near Macon. The pair was under observation approximately 75 per cent of the daylight time during the two-day period. Observations could be made throughout most of the day, because of the frequent chipping of the female. I believe that my observations were made during the early stages of pairing because of the date and because the six closest territorial males were unmated.

All paired males that I have observed during pre-nesting sang less often than at other times during the breeding season. Some such males sang only in early morning; others sang in early morning and a half dozen times or less in the remainder of the day. During the early morning song period the Macon male sang both complete and incomplete songs, but I heard him sing no muted (whisper) songs during the two-day observation period.

The Macon pair ranged over a territory of about 1.5 acres. One side of the territory bordered the Ocmulgee River, which at that point was approximately 75 yards wide. Another side was contiguous to a territory occupied by an unpaired male. One side of the neighboring bird's territory also bordered the river. An unpaired male held a territory immediately across the river. The river appeared to be an effective barrier as none of the four birds studied was seen to cross it during the two days of observations.

Hostile encounters between the neighboring paired and unpaired males occurred twice one day and four times in the other day of observations. During these encounters the female of the paired bird remained close to her mate, but within her territory.

The pair spent the day mostly on the ground within 20 feet of each other, often foraging 3 to 4 feet apart. Courtship feeding was not observed. The foraging pair was presumably aided in keeping close together by the frequent *chipping* of the female.

On one occasion a third bird, presumably a female, joined the pair in feeding on the ground for about three minutes. The visiting female was not chased, but the paired female *chipped* constantly until the visitor left the area.

What may have been a form of courtship display, in which the male flew down to the female and either pecked her rump feathers or pounced on her, occurred about three times each hour throughout the day.

After observing this behavior a few times, I could always anticipate when it was going to happen. The male, feeding on the ground usually within 10 feet of his mate, would discontinue feeding and mount a branch or fallen cane pole, usually from 6 to 12 inches above the ground. Then he remained virtually motionless in a crouched position for 1 to 5 minutes facing and presumably watching the female feeding on the ground. In this position the body feathers of the male were fluffed out, particularly on

the sides, and his head was drawn in close to his body. Occasionally he would slowly move his head slightly to one side. If the female moved too far out of range the male would shift to a closer perch and continue his crouched stance. The male's performance reminded me of a cat (*Felis*) getting ready to pounce on its prey. The male would then fly to the female and either peck at her as they moved along the ground for a distance of 2 or 3 feet; or he would pounce upon her and they would tussle or flutter together on the ground like two birds in combat. These encounters normally lasted less than 10 seconds. During the chase the female responded with a faint *tweet-tweet-tweet*. The female made no attempt to leave the ground in the course of this action or immediately following it. The pair then started feeding quietly within a few feet of each other.

Nice (1943:174-175) reported pouncing in the Song Sparrow (*Melospiza melodia*) as a form of courtship display, ". . . confined typically to the early stages of the nesting cycle . . ." The male ". . . suddenly flies down to his mate, collides with her, and immediately flies away with a loud song. At times he hits her severely . . ." And Howard (1929:22) observed that following the sexual chase, recently paired Yellow Buntings (*Emberiza citrinella*) flutter together on or near the ground, or peck each other as they rise in perpendicular flights, like males when fighting.

Howard (1929) believes that the sexual chase and pouncing shows that the male is ready to copulate (although the female is not yet ready to receive him). Based on Song Sparrow observations Nice (1943:174-175) states that pouncing by the Song Sparrow early in the season ". . . has no immediate connection with copulation . . . Pouncing on the mate occurs during the long period while song is inhibited and also during [nest] building. It may be a technique of the male for impressing himself upon his mate during the time of silence, of making his presence keenly felt."

NEST BUILDING

Nest building at Macon, Georgia, and Pendleton Ferry, Arkansas, started about three or four weeks after the first males arrived on the breeding grounds. A completed nest ready for eggs was found at Macon on 27 April 1946, and nests with full clutches were found by 3-4 May 1945. A nest containing one Swainson's egg and three Brown-headed Cowbird (*Molothrus ater*) eggs was found at Pendleton Ferry, 1 May 1967. The nest was probably constructed during the third week in April.

Based on observations on the Allegheny Plateau near Charleston, West Virginia, Sims and DeGarmo (1948:4) stated that nest building begins about two weeks after arrival on the breeding grounds. They found a completed nest as early as 1 May.

The earliest nesting is reported by Wayne (1910:150) who collected eggs containing small embryos on 28 April at Charleston, South Carolina. Perhaps the latest date is a nest with slightly incubated eggs found on 13 July 1886 at Savannah, Georgia (Perry, 1886:188).

In canebrakes the nest is rarely located in the densest part of the stand but nearer the edges where the stands are thinner and the cane poles are smaller. Only one of 12 nests that I observed was in a dense stand. Nests found by Howell (1928:284) in Alabama were similarly located. In a mature mountain cove hardwood forest at Charleston, West Virginia, Sims and DeGarmo (1948:4) found that in selecting a site, “. . . the bird avoids placing the nest in dense cover, yet in all instances, a patch of some type of such cover is within a distance of twenty-five to fifty feet. In many cases, this thicket is a growth of greenbrier but may be grape, honeysuckle, blackberry or bittersweet. There appears to be a definite effort to locate the nest in such a manner that it is in close proximity to a screen of protective cover.”

All nests that I found in territories in which I determined the boundaries through systematic measurement were inside of the territory. However, often they were near the edge, or the male spent most of his time in an area to one side of the nest. Sprunt and Denton (Griscom and Sprunt, 1957:51) had this to say relative to the location of the nest in the defended territory: “The territory defended by the male is used primarily for mating and feeding and not for nesting. The nest itself is usually located along the margin of the territory but may be entirely outside of it, . . .”

The Swainson's Warbler builds a large and rather bulky nest, apparently larger than that of most warblers that nest above the ground. The nest, usually placed at a height of 2-6 feet from the ground, is built by the female from materials gathered close to the nest site. During a sustained working period, one bird averaged about one trip per minute. Nests that I have seen under construction from the beginning took parts of two or three days to complete. The birds worked at nest building mostly in the forenoon.

Nests are constructed of a rather wide assortment of materials, but there is selection of certain plant parts. The number of species of plants represented in a nest somewhat depends on the composition of the forest in which the nest is located. There seldom were more than a dozen species of plants represented in the nests I examined. The number of pieces of plant parts in a Pendleton Ferry, Arkansas, nest totaled 418; the number in a Dismal Swamp, Virginia, nest was 323. Most pieces were in the lining of the cup. Sticks are seldom used in nests, and the few that occur in some almost seem incidental. But the first of three nests built by the same female in a single season in the Dismal Swamp, Virginia, contained a great many sticks, which is the reason that it weighed more than the second or third nests.

In canebrakes the foundation of a nest is often a bunch of dead leaves that have lodged in the axils of a cane stalk. The Dismal Swamp female referred to above

used the relatively large leaves of swamp magnolia (*Magnolia virginiana*) as a platform for each of her three nests. The nests were located at sites where several greenbrier (*Smilax* sp.) vines crossed a horizontal limb of a shrub so that the half dozen magnolia leaves formed a rather level base. Deposited upon these magnolia leaves were the dried leaves, sticks, vines, and tendrils that formed the rather loose outer layer of the nest. Most of the leaves were swamp magnolia, red maple (*Acer rubrum*), red bay (*Persea borbonia*), and greenbrier. Most of the sticks were greenbrier.

The next layer was more compactly structured, consisting almost entirely of decomposed or skeletonized leaves of the swamp magnolia. This layer formed the outer shell of a cup composed of finer materials in which the eggs were deposited. In positioning these leaf skeletons, the tips of the leaves were placed near what became the bottom of the cup (bowl), and they were then drawn toward the rim at a gradually sloping angle to the curve of the cup. All of these leaves were placed in a regular pattern, being drawn clockwise from near the base on one side of the cup to emerge and protrude from the rim at almost the opposite side. All of the protruding petioles were then pointing away from the circle of the rim at a narrow angle clockwise. This layer was constructed similarly in all three nests. Swamp magnolia leaves being elongated in shape, arc well suited for this part of the nest structure. Next to this layer of magnolia leaves was a layer of eypress twigs with needles.

The inside of the cup was lined with rootlets (unidentified) and petioles of red maple flowers. All three of the Dismal Swamp nests were lined with these petioles. Apparently they are a preferred item for the lining as I have also found them in nests at Macon, Georgia. Chapman (1907:53) reports that J. N. Clark found them in linings of nests of the Worm-eating Warbler (*Helmitheros vermivorus*) in New Jersey.

The Dismal Swamp female that built three nests in one season used fewer materials in constructing each succeeding nest; thus the nests were progressively lighter. The dry weights of each was 47.7, 39.8, and 26.3 grams. A Pendleton Ferry, Arkansas, nest weighed 24.3 grams.

Dimensions of the Arkansas nest were as follows: greatest outside diameter 15.0 cm; inside diameter of cup 4.0 × 5.0 cm; outside depth 7.8 cm; inside depth of cup 4.2 cm.

EGG LAYING, CLUTCH SIZE, AND INCUBATION PERIOD

At two Louisiana nests, there was a lapse of two days between the completion of the nests and the laying of the first egg. Eggs were laid daily until the clutches were complete. Incubation began with the laying of the last egg in the clutch.

Clutch size in six Georgia nests was as follows: 4 of 3 eggs and 2 of 4 eggs. The somewhat globular eggs are white; slightly spotted eggs are rarely found (Wayne, 1910:149).

By marking eggs, the incubation period of nests at Augusta, Georgia was determined to be 14–15 days (J. Fred Denton, pers. comm.).

COWBIRD PARASITISM

In some parts of its breeding range, the Swainson's Warbler may be rather heavily parasitized by the Brown-headed Cowbird. During the first

week in May 1967, at Pendleton Ferry, Arkansas, I located three Swainson's Warbler nests, all of which were parasitized. At one of the nests the warbler was incubating three Cowbird eggs and one of its own. Three days later it was still incubating, but one of the Cowbird eggs and its own egg were missing.

Kirn (1918:97-98) reported several parasitized nests in Copan County, Oklahoma; Sims and DeGarmo (1948:5), in the course of three years, found three of 18 nests parasitized at Charleston, West Virginia.

BEHAVIOR DURING INCUBATION PERIOD

I obtained most of my information on behavior during the incubation period from a nesting pair in the first week of May at Pendleton Ferry, Arkansas. The pair was the one mentioned above whose nest contained three Cowbird eggs and one warbler egg. This nest was located about two feet above the ground between two cane poles. Incubation was performed by the female.

During incubation the Pendleton Ferry female spent about 78 per cent of her daylight time on the nest. The average time on the nest was 70 minutes; the average time off was 19 minutes. The longest period recorded on the nest was 110 minutes, the shortest, 30 minutes. The longest period off the nest was 25 minutes, the shortest, 15 minutes. At Tifton, Georgia, Norris and Hopkins (1947:8) observed a female that remained on her nest continuously for nearly four hours. Lawrence (1953:138), summarizing studies of six wood warblers, found that attentiveness ranged from 67 to 83 per cent.

The Pendleton Ferry female, unlike others that I have seen, always sat in the same position when incubating. She left the nest in the same direction but did not always feed in the same area. She fed as far as 75 yards from the nest but usually about 30. She fed both alone and with her mate. On one occasion the male which had not sung for more than an hour flew to within 50 feet of the nest and sang two songs. The female *chipped*, left the nest, and the two flew off together to feed. Sometimes on leaving the nest the female flew out to about 30 yards from the nest where she *chipped* several times presumably to attract the male. Upon returning to the vicinity of the nest the female invariably *chipped* two or three times just before settling down on the nest.

A female in the Dismal Swamp was often fed by her mate when she left her nest during the incubation period. She would follow the male on the ground like a fledgling following its parent. The male, moving about with cocked tail, would gather food and present it to her.

During the several days of my observations, the Pendleton Ferry male

never visited the nest. He did not come closer than 40 feet, and usually stayed more than 100 feet distant. However, Norris and Hopkins (1947:8) and Sims and DeGarmo (1948:5) reported males visiting incubating females at the nest. At dusk the male was usually seen closer to the nest (40–50 feet) than during the lighter part of the day. He fed and sang in all areas surrounding the nest. He did not sing as much as an unmated male in an adjacent territory.

CARE OF YOUNG

My information on the care and feeding of nestlings is based on observations made during a 7-hour period in the Dismal Swamp on 7 July 1967.

Between 09:45 and 16:45 the 3-day old nestlings were fed 14 times, eight by the male and six by the female. The intervals between feedings ranged from 9 to 59 minutes.

The female was at the nest 53 per cent of the time brooding the young and sometimes standing on the rim. If she was brooding when the male came to the nest she would move to the rim while he fed the young. Of this pair only the male removed fecal sacs from the nest; however, at a Macon, Georgia, nest, the female also removed fecal sacs, sometimes by swallowing them.

The male always approached from the same direction and worked his way slowly through the undergrowth until he was 2–3 feet beneath the nest, then he hopped up to the rim. The female approached from various directions, and flew directly to the rim of the nest from 20–30 feet out. On three occasions the male and female departed from the nest at the same time. Each time they flew in different directions.

Sims and DeGarmo (1948:5) found that at several West Virginia nests, young left after 10 days. At Augusta, Georgia, the young remained 12 or more days (Griscom and Sprunt 1957:53). Young that I observed at Macon, Georgia, fledged at 10 days.

Fledglings of another Dismal Swamp brood, just two days out of the nest, were fed only by the female during my two days of observation. The male was usually within 100 feet of the young, and sang much of the time.

On three occasions, just as the female was about to feed one of the fledglings, the male pounced on her.

DISCUSSION

Nesting success for this species appears to be low. Of 15 nests for which I have complete records, only 5 were successful. Sims and DeGarmo (1948:5) reported only 6 of 18 nests as successful.

Of the several factors working against nesting success, three appear to be most important. One is the vulnerability of the Swainson's Warbler's

poorly concealed nest, which is placed close to the ground and contains white eggs. Other breeding parulids that nest in similar habitats, the Black and White Warbler (*Mniotilta varia*), Worm-eating Warbler, Ovenbird, Louisiana Waterthrush (*Seiurus motacilla*), Kentucky Warbler (*Oporornis formosus*), and Hooded Warbler (*Wilsonia citrina*) have speckled eggs and usually conceal their nests better.

The large bulky nest of the Swainson's Warbler, constructed mostly of leaves, apparently is quite suitable as a home for the wood mouse (*Peromyscus* sp.). I have known of several new Swainson's Warbler nests taken over by mice during the egg-laying stage. However, I do not know whether the birds deserted their nests prior to or because of the presence of mice. Legg (1946:25) also noted evidence (scats) of mouse use of a deserted Swainson's Warbler nest.

In another paper (Meanley, 1966:164) I mentioned the effects of flooding on Swainson's Warbler productivity during the nesting season in floodplain forests of the Atlantic Coastal Plain.

And the Swainson's Warbler may have an even greater time maintaining its numbers as the Cowbird continues to extend its breeding range farther into that of the Swainson's Warbler (Webb and Wetherbee, 1960).

SUMMARY

The Swainson's Warbler is one of the least known of southern birds. Although fairly common in some parts of its summer range, observations of its breeding biology have been made by very few persons. The present study was conducted mostly at Macon, Georgia; Pendleton Ferry, Arkansas; and Dismal Swamp, Virginia.

In central Georgia and east-central Arkansas, Swainson's Warblers usually arrive on their territories during the first two weeks in April. Territories in several localities ranged in size from 0.3 to 4.8 acres. A color-marked Arkansas male occupied the same territory for at least four months. Hostile encounters between territorial male Swainson's Warblers usually take place along the boundary of adjacent territories. Paired males were more aggressive than unpaired males. Toward the end of an encounter one of the two males would usually perform a display in which the wing and tail feathers were spread and the tail vibrated. Following boundary encounters males drifted back onto their territories and usually sang unbroken courses of songs for several minutes.

During pre-nesting at Macon, a mated pair spent the day mostly on the ground within 20 feet of each other, often foraging 3 to 4 feet apart. What may have been a form of courtship display, in which the male flew from a perch down to the female and either pecked her rump or pounced on her, occurred about three times each hour throughout the day. During this period the male sang less than at other times during the breeding season.

First nests are usually built by the first week in May. Although other investigators reported finding nests of this species outside of the defended territory, all nests that I have found were within the territory. The large, bulky nest of this species usually is placed 2-6 feet above the ground. It is built by the female from materials gathered close to the nest site; and takes two or three days to complete.

Three and occasionally four white eggs are laid. The female incubates for 14–15 days. The Cowbird parasitizes nests in some parts of the breeding range of the Swainson's Warbler.

During incubation the female spends about 78 per cent of daylight time on the nest. Both sexes feed young and clean nest. Young remain in nest from 10–12 days.

ACKNOWLEDGMENTS

I am grateful to Dr. Paul A. Stewart of the Agricultural Research Service, U.S. Department of Agriculture, for reviewing the manuscript; and to Mrs. Nancy Coon of the Patuxent Wildlife Research Center for the diagram of the territories.

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